Can *in-situ* experience compensate for hatchery-deprivation?

Enhancing post-stocking survival of juvenile Atlantic salmon.

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Abstract

Can *in-situ* experience overcome hatchery deprivation?

Enhancing post-stocking survival of juvenile Atlantic salmon

Michelle C LeBlanc

Atlantic salmon (*Salmo salar*) exhibit maladaptive behaviour when stocked into natural streams following one generation in a hatchery setting, reducing post-stocking survival. These behavioural patterns are commonly attributed to 'hatchery selection', where maladaptive phenotypes arise from the inadvertent selection of behavioural traits, lack of experience caused by captivity, or a combination of both. 'Life skills training', in which hatchery-reared fish are conditioned to exhibit appropriate behaviour responses, may increase post-stocking survival.

A semi-natural field experiment, using *in-situ* mesh enclosures, compared wild-caught juvenile salmon to hatchery-reared counterparts from the same population. Fish were observed for antipredator, foraging, and territorial defense responses. Results showed no significant differences between wild and hatchery raised fish, although behaviour was significantly different between years. Overall, week long trials were insufficient in separating significant differences between strains, indicating one generation in captivity may not create major behavioural separation between wild and hatchery fish from the same population, or that more than one week is required for differences to become apparent. Behavioural response training protocols are suggested for hatchery raised experientially deprived fish destined for stocking.

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Experiment: Can *in-situ* experience compensate for hatchery-deprivation?

Enhancing post-stocking survival of juvenile Atlantic salmon.

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Introduction

Many wild fish stocks have been depleted by human activities, such as overfishing and habitat degradation (Brown & Day 2002; Fraser 2008). Species such as Atlantic cod (*Gadus morhua*, Sutherland 1998), Beluga sturgeon (*Huso huso*, Akbulut *et al.* 2011), Atlantic redfish (*Sebastes fasciatus*, Devine & Haedrich 2011), Atlantic halibut (*Hippoglossus hippoglossus*, den Heyer *et al.* 2013), Adriatic sturgeon (*Acipenser naccarii*, Boscari *et al.* 2014), and Atlantic salmon (*Salmo salar*, de Mestral & Herbinger 2013) have all seen significant declines in recent decades. In response, captive breeding programs have been set in place to counteract these declines, enhance threatened populations, reintroduce extirpated populations, and conserve genetic diversity of fragmented populations (Salvanes & Braithwaite 2006; Christie *et al.* 2012; Stark *et al.* 2014). Establishing captive breeding efforts before populations become critically endangered, aids in conserving as much genetic variability as possible, in the hopes that the population will be maintained until it can naturally sustain itself (Fraser 2008; Saikkonen *et al.* 2011).

In the case of threatened or endangered fishes, hatchery-reared populations are commonly stocked into natural waterways in an attempt to prevent population declines for at-risk or commercially valuable fish species (Brown & Day 2002; Fraser 2008). Populations experiencing pressures from habitat degradation (fragmentation or loss), overexploitation, and pollution are particularly vulnerable *(Olla et al.* 1998; Fast *et al.* 2008). Typically, large numbers of fish are reared and released en-masse, however, in recent years, more attention is being paid to stocking individuals of higher quality, both genetically and behaviourally, (Brown & Laland 2001). However, many of these stocking programs have been met with limited success (Olla *et al.* 1998; Fast *et al.* 2008; Fraser 2008). Although effort has been taken to enhance and supplement populations, stocked hatchery fish often have poor survival (Olla et al. 1998; Deverill *et al.* 1999; Brown & Day 2002; Berejikian *et al.* 2003; Chittenden *et al.* 2010). In particular, Atlantic salmon populations have been extirpated from a majority of sites within their original range, and are currently listed as endangered or special concern by COSEWIC (COSEWIC, 2010). De Mestral and

Herbinger (2013) have found that Atlantic salmon no longer spawn in 97% of their original nursery rivers on the Bay of Fundy, with population declines as high as 99% in the past 40 years. The Atlantic salmon population in this study is listed under the Gaspé-Southern Gulf of St-Lawrence and is listed as a Special Concern (COSEWIC, 2010). Additionally, 2014 return numbers for large adult Atlantic salmon in the Miramichi river were just 8940 individuals (95% CI 5600-14700), the lowest number since 1992 (DFO, 2015). Inadequate knowledge of the ecological interactions that contribute to the shaping of behavioural responses in fishes may result in the production of fish unprepared to cope with the natural environment, resulting in high mortality rates shortly after release (Brown & Day 2002).

Recently, research has focussed on identifying the causes of these post-stocking survival deficits in hatchery-raised fish (Olla *et al.* 1998; Brown & Day 2002; Jackson & Brown 2011; Brown *et al.* 2013). Hatchery facilities provide a controlled, captive environment with ideal conditions for raising large numbers of fish. These fish are eventually released into the natural environment, with the hope that they will supplement the local population. Hatchery selection, including relaxed selection, and inbreeding are found to be factors that reduce post-stocking survival, by selecting traits beneficial in captivity that may be maladaptive under natural conditions (Brown & Day 2002; Salvanes & Braithwaite 2006; Fraser 2008). The process of hatchery selection has received considerable attention in recent years (Brown *et al.* 2013), and involves either the selection of specific phenotypes, the relaxation of natural selection pressure, or inadvertent selection during the reproductive process (Huntingford 2004; Bert *et al.* 2007; de Mestral & Herbinger 2013).

Reduced mortality in hatchery conditions is another likely cause of observed behavioural differences. In the wild, fish must survive fluctuating environmental conditions, predation threats and competition, which results in high levels of natural mortality among the early life history phases. However, hatchery fish survive in much higher numbers due to ideal rearing conditions devoid of risk. Miramichi Salmon Association (M. Hambrook, personal communication), reports survival rates from

hatching to release of 94% in 2013, and 75% in 2014; numbers which agree with the 85-94% survival rates in hatcheries, verses 1-5% survival rates from hatching to smolt, within natural populations (Araki et al. 2008).

The high levels of mortality seen in hatchery fish shortly after their release may be a result of delayed mortality, in which fish without appropriate phenotypes are selected against suddenly, instead of during earlier life stages (Huntingford 2004; Jonsson & Jonsson 2006). In addition, differential experience also adds to the factors working against the survival of hatchery fish. In the hatchery, fish are not exposed to the same developmental environment as their wild counterparts, and since experience is a large factor in behavioural response development, hatchery fish are thus unable to develop the same behavioural response patterns (Brown *et al.* 2003a; Huntingford 2004).

Given the combined effects of hatchery selection, reduced mortality, and differential experience, hatchery fish are more likely to display behavioural deficiencies such as reduced foraging efficiency, antipredator behaviour, or territory holding ability (Olla *et al.* 1998; Deverill *et al.* 1999; Alvarez & Nicieza. 2003; Jackson & Brown. 2011; Rodewald *et al.* 2011; Tatara & Berejikian 2012; Neuman *et al.* 2013) when stocked into natural waterways. Released fish must quickly learn several life skills after stocking, in order to survive. Most importantly, they must learn how to respond appropriately to predators (Alvarez & Nicieza 2003), how to forage efficiently (Reiriz *et al.* 1998; Rodewald *et al.* 2011) and how to acquire and maintain a territory (Deverill *et al.* 1999; Tatara *et al.* 2008), shortly after release to avoid starvation or predation. Huntingford (2004) demonstrates that even fish of the same genetic background may display different behavioural responses when reared in different conditions. These differences arise from the combined effects of a lack of relevant experiences, and habituation to the hatchery environment. When combined with hatchery selection, these behavioural effects combine with genetic relaxation to further solidify these behavioural deficiencies, and potentially create behavioural divergence (Alvarez & Nicieza 2003). Jackson & Brown (2011) highlight the combination of hatchery

selection and differential experience, which act together to influence the behavioural phenotypes of hatchery reared fish that have only spent one or two or fewer generations in captivity.

Behavioural deficits among hatchery-raised salmonids

There is growing evidence of behavioural deficits among hatchery reared fishes, which may lead to low observed post-stocking survival. Initially, when compared to wild fish, hatchery-raised fish forage less efficiently, and although the rate of foraging may be high, handling of prey items is often poor or attempts may be made on incorrect, or non-food items (Reiriz *et al.* 1998; Brown *et al.* 2003b; Huntingford 2004; Fast *et al.* 2008). Luckily, Atlantic salmon have previously shown the ability to quickly alter prey choice when given access to wild prey items, indicating an innate attraction to live prey (Sundstrom & Johnsson 2001; Rodewald *et al.* 2011). Likewise, Brown *et al.* (2003a) showed the ability of hatchery reared Atlantic salmon to quickly generalize prey items with as few as 6 exposures, but only when the fish had been reared in an enriched environment. This is an important detail, because hatchery-reared salmonids are typically not exposed to live or novel food items until they are released (Brown *et al.* 2003a; Jackson & Brown 2011). Therefore it is critical to gain experience with different prey items in order to maintain optimal foraging under varying environmental circumstances (Brown & Laland 2001; Massee *et al.* 2007).

Secondly, territorial animals seek profitable environments that maximize energy gain and minimize expended energy (Deverill *et al.* 1999). Often, newly released hatchery salmonids fail to disperse from the release site, or are more aggressive than their wild counterparts, leading to increased competition for limited resources. They are also more likely to select risky or energetically costly positions within the water column, such as close to the surface or in high flow areas (Brown & Day 2002). As a result, hatchery-raised salmonids may suffer higher costs associated with defending territories that are either above or below an optimal size. Released hatchery fishes must be able to acquire and maintain a territory within the stream, in order to be successful in the natural environment. However,

they were raised in overcrowded conditions, which increases agonistic behaviour and a decreases the ability to successfully defend a territory (Brockmark *et al. 2007;* Brockmark *et al.* 2010; Olla *et al.* 1998). Without previous experience defending territories, hatchery-raised rainbow trout (*Oncorhynchus mykiss*) suffer declines in growth rate when introduced to artificial stream environments, which may also translate into increased mortality after release (Deverill *et al.* 1999). These findings have negative implications for newly released hatchery-raised fish, which are likely to have difficulties assessing, selecting, and maintaining territories.

Finally, predation is found to be the leading cause of death in recently released salmonids (Olla *et al.* 1998; Brown & Day 2002). Predator recognition and avoidance consists mainly of accumulated, learned behavioural responses, which are unfamiliar to hatchery-raised fish as they are predator naïve when placed into wild environments. However, learning is costly as newly stocked individuals must survive their initial encounters with predators in order to gain experience (Dall *et al.* 2005).

Life skills training

One commonly advocated approach to overcome hatchery deficits is 'life skills' or predator recognition training, in which hatchery fishes are conditioned to exhibit appropriate behavioural response patterns prior to release in order to overcome potential behavioural deficits (Brown & Smith 1998). For example, Brown & Laland (2001) describe that mortality of hatchery fish is often highest within days of release, and that smolts, fish which have undergone physiological, morphological and behavioural changes to prepare for ocean life, that survive three weeks in the wild are likely to continue to avoid mortality. However, life skills training currently does not translate well into improved survival, as attempts to provide predator recognition training to hatchery fish has been met with limited success in improving post release survival (Brown *et al.* 2013). Brown & Laland (2001) suggest the use of environmental enrichment, in combination with opportunities to engage in natural foraging and antipredator behaviour, can help fish overcome the behavioural deprivations associated with hatchery-

raised fish. One alternative to hatchery-based life skills training would be to stock hatchery fish into semi-natural enclosures prior to their release into natural streams. This is hypothesized to allow hatchery fish the opportunity to gain relevant experience (Brown *et al.* 2013).

Thesis Goal

Here, I tested the prediction that *in-situ* experience will allow hatchery-reared salmon to overcome documented behavioural deficits. Additionally, I manipulated the perceived environmental risk level using conspecific chemical alarm cues or a stream water control, which I introduced twice daily into the enclosures. These introductions were used to investigate if the differences of perceived predation risk will enhance or suppress the development of natural behavioural responses in young-of-the-year (YOY) first generation hatchery-raised Atlantic salmon. Furthermore, by exposing half the enclosures to ambient predation risk conditions and the other half to enhanced risk using conspecific alarm cues; I tested the role of background predation threat on antipredator behaviour and learning. Previous studies have shown that high-risk environments increase learning and retention, and therefore lead to the faster acquisition of skills (Brown *et al.* 2013). Behavioural responses will be observed twice daily, and will consist of ten minute observations, where territorial placement, foraging attempts, time spent on the substrate and the number of active fish in the enclosure will be recorded. I hope to discover how gaining ecologically relevant experience *in-situ* will impact the behavioural deficits critical to survival in hatchery reared YOY Atlantic salmon.

Predictions

I predict that wild-caught fish will display the strongest antipredator responses when exposed to alarm cue. This will cause them to hold and maintain larger territories, and maintain the highest foraging rate. I expect all of these behaviours to be lower in hatchery-raised fish compared to wild, but I

also expect improvements for both fish strains to occur over the 7 days *in-situ*. Likewise, wild-caught fish are expected to grow at a faster rate, and to be more active than their hatchery counterparts.

Wild fish are accustomed to acquiring and holding territory and defending it from others, therefore I expect that they will more effectively maintain larger territories *in-situ* compared to hatchery fish (Fraser 2008). When presented with high-risk environments, I expect territory size to be smaller when compared to ambient risk, regardless of strain (Kim *et al.* 2011). Foraging rates for wild-caught fish are expected to remain consistent over 7 days *in-situ*, as previous experiences with wild prey within the natural environment will provide them with the experience necessary to forage efficiently (Brown *et al.* 2003a). Conversely, hatchery fish be will experiencing novel conditions and food types, and are likely to display lower foraging rates. I also predict that foraging rates will be reduced for both wild and hatchery fish that experience an increased predation threat, due to increased predator avoidance.

Materials and Methods

Test Site

The experimental site is located on the Little Southwest Miramichi River (46°52'N 66°06'W) in Northumberland County, New Brunswick, Canada (Figure 1) over two successive years from June 27th - August 23rd 2013 and July 2nd - July 27th 2014. Catamaran Brook is a common study site for the behaviour of Atlantic salmon, as it hosts a habitat research station and a naturally spawning population of wild Atlantic salmon (Girard *et al.* 2004; Kim *et al.* 2011; Steingrimsson *et al.* 2008).

In 2013, four test sites were established approximately 100 meters downstream from the confluence of Catamaran Brook. Each test site contained net enclosures located approximately 10 meters apart, 3 meters from the shoreline. Test sites were selected for similar characteristics, such as sediment, water flow, and canopy cover. Water temperature, depth (using a meter stick), cloud cover and water velocity (mid-depth between the substrate and surface) were recorded daily. Cloud cover

was estimated by measuring directly above the test sight using an 8 square grid, with zero being no cover and eight being full cover. This amount was later translated into percent coverage. Velocity was measured using a Flo-Mate velocity meter in 2013 and by float velocity in 2014.

Experimental Setup

Net enclosures (4 in 2013, 6 in 2014), measuring 6 m x 1 m x 0.75 m with a 3 mm mesh size, were anchored in the river using hollow metal poles, and filled with cobble and gravel to provide refugia and mimic the natural streambed. Flagging tape was placed every 25 cm along one length and one width of the enclosure, creating a grid pattern consisting of 96 squares (25 cm^2 each), to help visualize and record territory use. This grid system simplified the recording of the territorial positions onto waterproof data sheets. The positioning of each central placement was measured with a maximum Y coordinate of 600 cm, and a maximum X coordinate of 100 cm, which represented the enclosure area on the grid sheet. Hatchery-reared, YOY juvenile Atlantic salmon were obtained from the Miramichi Salmon Association (MSA) hatchery located in South Esk, New Brunswick. Fish were transported on a weekly basis to the research site in a 20L plastic container containing hatchery brook water. Upon arrival at the test site, hatchery fish were released into a 40L plastic holding bin (0.8 m x 0.46 m x 0.34 m). Wire mesh (3.1mm) replaced the front and back of the holding bin, which allowed free flowing water and acclimation to stream conditions. Substrate consisted of sand, pebbles and rocks from the stream, which lined the holding bins, provided shelter, and anchored the bin on the streambed. The bin was also tied to a tree on the shoreline to prevent loss in the case of a flood.

The YOY hatchery-reared (HR) Atlantic salmon were first generation offspring from inhabitants of Little Southwest Miramichi River (LSW). First generation (F1) fish are defined as the offspring of wild-caught parents that are used as brood stock. Wild spawning adults are collected annually during their Autumn migration to their native spawning stream, and then used by the MSA hatchery as brood stock (M. Hambrook, personal communication).

Wild-caught YOY Atlantic salmon were captured with a dip net while snorkelling in Catamaran Brook (CB), a tributary of the Little Southwest Miramichi (Cunjak *et al.,* 2013). Catamaran Brook was used as the source stream due to its ideal physical conditions, and because there is no reported stocking of hatchery-raised fish in this river. All captured juveniles were purely of wild origin and were classified as WC (wild-caught). However, there are no barriers to prevent interbreeding between LSW and CB populations, and therefore the likelihood of sub-population differences between these populations. Riddell et al. (1981) reported different morphological adaptations to environmental conditions in two populations from Little Southwest Miramichi tributaries, providing evidence of fine scale local adaptation within this system.

Six fish were placed into each enclosure, at a density of 1 fish m^{-2}, which is within the natural observed density of Atlantic salmon (Imre *et al.* 2005). All fish were weighed (to the nearest 0.1g), measured from snout to medial caudal fin ray (to the nearest 0.01mm), and tagged with Visible Implant Elastomer (Northwest Marine Technologies Inc.) on the dorsal surface near the head, dorsal or caudal fin, to enable individual recognition, and were transferred to a holding bin and held for a maximum of three days (72 hours) before being placed in an enclosure. All fish were transferred a holding bin and were held a maximum of three days (72 hours) before being placed in an enclosure. Fish were given 24 hours to acclimate to the enclosure before testing. Any fish that died within its first 24 hours within the enclosure was replaced.

Stimulus Preparation

Alarm cue was collected from a whole body homogenate obtained from hatchery reared LSW F1 Atlantic salmon, on June 29th 2013. Fish were humanely killed by a single blow to the head immediately after their removal from hatchery tanks, in accordance with Concordia University Animal Care Committee Protocol AC-2013-BROW. Fish were then measured, from snout to medial caudal fin ray; then the head and tail were removed and the body was chilled in an ice water beaker. Bodies were

homogenized and filtered through polyester filter floss, then diluted with untreated well water. The homogenate was chilled in neutral well water, resulting in a concentration of 0.09 cm^2 ml^{-1} was frozen into 50ml and 20ml aliquots at -20^{O}C. In total, 2327 mL (232.706 cm^2 of skin) of alarm cue was used. It has been previously shown that alarm cue derived from whole body homogenates can be reliably used as an indicator of predation risk (Brown 2003; Brown & Smith 1997; Brown *et al.* 2010; Jackson & Brown 2011). This alarm cue preparation method has been shown to effectively evoke alarm responses in Atlantic salmon (Leduc *et al.* 2006; Kim *et al.* 2009; Jackson & Brown 2011; Elvidge 2013).

Trials

Field trials were performed between July 2nd - August 25th, 2013 and July 2nd – July 27th 2014. All test fish were acclimatized in holding bins for 24-72 hours before transfer into net enclosures. This allowed time for fish to adjust after their transfer, and to adapt to the change in environmental variables. In this way, all fish were exposed to the same pre-testing conditions. A total of four treatments were used, with enclosures receiving high-risk treatments placed downstream from stream water controls, to avoid potential contamination. Twice daily injections of stimulus were performed a minimum of 30 minutes before an observation period. Enclosures were exposed to either 50mL of alarm cue (AC) or 50mL of stream water (SW), at 50% water column depth for a total of 100mL per day of AC or SW. These cue administrations simulated high or ambient background predation risk levels. Behavioural response observations were 10 minutes in duration, and were conducted twice daily. This 2x2 factorial design, combined two population strains (hatchery or wild), and two risk treatment regimens (high or low-risk), for a combination of four treatments. In 2013, 4 blocks with 4 enclosures were performed, for a total of 4 replicates per treatment, while in 2014, 2 trials with 6 enclosures were performed, for a total of 3 trials per treatment. Overall, 7 trials were conducted for each of the four treatments.

Observations were performed standing at an angle above the enclosure. After each seven day trial, all test fish were removed from the enclosure by a snorkeler, and were weighed and measured to the medial caudal fin ray. Fish were then released into the Little Southwest Miramichi River, as per stocking protocol. No hatchery fish were released into Catamaran Brook. The magnitude of antipredator response was determined using two main behavioural response measures: number of foraging attempts, and time on substrate (seconds). These behavioural response measures have been shown to accurately quantify antipredator response in Atlantic salmon (Leduc *et al.* 2007; Kim *et al.* 2009; Jackson & Brown 2011). Foraging attempts were counted when a fish moved a minimum of half a body length, and performed a biting action towards a food item in the water column, on the substrate, or at the water surface. Time on substrate was defined as the time an individual spends motionless on the substrate, whether hiding, or maintaining a territorial position. Daily foraging counts consisted of 10 minute foraging observations in the morning (9am-12pm) and evening (17:30pm – 19:30pm).

2013 vs. 2014 Protocol

In 2014, the area of testing had to be changed due to shifts in the stream bed and sediment placement over the winter, which made the previous testing location unsuitable for enclosures. In 2014, initially 4 enclosures were installed at the mouth of Catamaran Brook. After 2 days of observations, Hurricane Arthur damaged the enclosures and testing was suspended for 8 days. Afterward, 6 enclosures were deployed into Catamaran Brook. Using 6 enclosures, a trial and a half trial (4 treatments, plus 2 additional treatments) were run simultaneously for two weeks, with observations occurring on alternating days for 7 days, producing 3 trials per treatment. In 2013, a total of 4 trials were completed for each treatment, with one treatment per trial occurring per week, for a 4 week period. This produced results for 7 trials per treatment, for a total of 28 tested enclosures, and an equivalent total of 8 weeks over two field seasons. Each enclosure contained 6 fish, and a total of 168 fish were tested.

In 2014, the testing regime was altered slightly between years due to changes in the substrate, which made equipment installation impossible. On each day, behavioural response observations took place, and because of this change in protocol trials were able to be completed in one month (July in 2014), rather than two (July and August 2013). Additionally, fewer observations and growth rate data were collected in 2014, due to higher mortality rates of the fish in the enclosures. Greater amounts of fishing spiders (*Dolomedes tenebrosus*) were observed around the enclosures, which may have contributed to the increased losses.

Statistical Analysis

Territorial observations were recorded on an X, Y coordinates grid which represented the area of the enclosure. The open source software QGIS 2.2.0 was used to evaluate the territorial coordinates to 95% confidence interval. Multiple central placements were combined to create a Convex Hull (CH), which combined the central placements into one territory to create a total area per individual. Each central placement was input including a 10cm radius, due to the software's inability to recognise less than 3 points as a convex polygon. The average length of the fish used in this experiment was 37mm, thus a 10 cm radius reasonably falls within range of a defendable radius around a central foraging placement of 3.6 body lengths (Steingrímsson & Grant 2008).

Specific Growth Rate (SGR) in body weight (%) per day^{-1} was calculated from growth data using the formula:

$$SGR = \left(\frac{(ln\mathrm{W2} - ln\mathrm{W1})}{\mathrm{T2} - \mathrm{T1}} \right) x\ 100$$

where W1 represents initial weight at day 1, W2 represents the final weight at day 6 (2013) or 7 (2014) for each individual with growth rate data for the entire trial period. Data for growth was analysed separately from the behavioural responses, and was tested for assumptions of normality. The average

specific growth rates of all fish in the same enclosure, for the same treatment during the same trial (strains/cue combination), was calculated. This produced a total of 28 observations and 28 degrees of freedom. ANOVA was used to analyse SGR as the dependent variable, with cue, strain and cue*strain interaction as fixed factors, and year as a random factor.

The number of observed foraging attempts was expressed as a rate per minute. Time on substrate was recorded in seconds, and was then converted into to a percent time on substrate, in order to account for fish that became lost during an observation. To create a percent time on substrate, the length of time on substrate was divided by the total length of time the fish was viewed.

In this experiment, fish were randomly observed in each enclosure daily, due to the fact that not all fish were active at one time, or fish may have been active but not visible. This created replication by enclosure, with each enclosure containing up to six individual fish receiving one treatment. Therefore, any observation in the enclosure was considered an observation for that treatment regime (combination of strain and cue). The data for 'early' vs 'late' was pooled to ensure sufficient observations, as there were a small number of observations on day 1 and day 7. For the 2013 dataset, days 1-2 created 'day 1', and 5-6 produced 'day 7'. In 2014, days 1-3 created day 1, while days 5-7 produced day 7. An average from all observations of the same trial receiving the same treatment on the same day was produced, which created a total of 28 observations for both day 1 and day 7. Because of this, all statistical outputs have 28 degrees of freedom when analysed in ANOVA.

All behavioural response observations, activity, foraging rate, percent time on substrate, and area, were dependent variables, while year, strain (WC and HR), cue (AC and SW), and strain*cue interaction were fixed factors, and year was evaluated as a random factor. When significant differences were found between year, separate figures were created for each year. Each combination of treatment and trial was considered a unique grouping variable. Statistical analyses were performed using two-way ANOVAs in SPSS 20.

Results

Growth

Specific growth rate was significantly influenced by fish strain (hatchery vs wild caught) (ANOVA $F_{1\text{-}28}$ = 9.495, P = 0.005). Overall, hatchery fish grew significantly less than their wild counterparts, especially when presented with a high risk environment, while the growth of wild fish was similar, regardless of risk (Figure 2). Growth was not significantly affected by year, cue, or strain*cue interaction.

Behavioural Observations

Activity

Fish activity was not significantly affected by strain, cue or by a strain*cue interaction (Table 1). Year was found to significantly affect activity on day 1 (ANOVA $F_{1\text{-}28}$ = 4.60, P = 0.04), but not on day 7 ($F_{1\text{-}28}$ = 3.37, P =0.08), with higher activity levels in 2013 (Figure 3). Therefore, the number of active fish in the enclosures was not dependent on the threat level they experienced, or the location they originated from. Enclosures with wild fish under ambient conditions tended to have higher numbers of active fish than the other treatment combinations, which differed little from each other (Table 1).

Foraging

Foraging rate was found to be significantly affected by year on both day 1 (ANOVA $F_{1\text{-}28}$ = 6.75, P=0.02) and day 7 (ANOVA $F_{1\text{-}28}$ = 16.46, P=<0.00; Figure 4). Fish foraged at a higher rate in 2013, compared to 2014 (Figure 4). Foraging rate was not significantly affected by strain, cue or a strain*cue interaction (Table 1).

Time on Substrate

Time on substrate was significantly affected by year for day 1 (ANOVA $F_{1\text{-}28}$ =7.14, P=0.01), but not day 7 (ANOVA $F_{1\text{-}28}$ =0.28, P=0.60) (Table 1). Overall in 2013, fish spent more time on the substrate compared to 2014 (Figure 5).

Territory Size

Territory size was significantly impacted by year on day 7 (ANOVA $F_{1\text{-}28}$ =8.25 P=0.01), but not day 1 (ANOVA $F_{1\text{-}28}$ =0.00, P=0.99). Territories on day 7 were larger in 2013, than in 2014 (Figure 6). Strain, cue, and the strain*cue interaction did not significantly affect territory size (Table 1). All treatment combinations showed tendency toward increasing territorial areas after a week *in-situ*, with The majority of the territories were small, with the minimum allowable size for the QGIS program being 0.04m^2, additionally the majority of territory sizes were not over 1m^2.

Overall, no effect was found of strain or cue on behavioural responses in Atlantic salmon. However, year effects were pronounced throughout the results. Fish were found to be more active in 2013, on day 1 however, by day 7 similar activity levels were seen in both years. Foraging rates were higher in 2013, both on day 1 and day 7. However, this did not translate into higher growth rates; instead growth rate was mainly impacted by fish strain, with hatchery fish growing significantly less then wild counterparts. Fish were found to spend more time on the substrate in 2013, on day 1 whereas, by day 7 time on substrate was similar regardless of year. Additionally, larger territories were seen in 2013, on day 7, whereas on day 1 territory sizes were similar regardless of year.

Discussion

Differences between years were observed for all behavioural responses, and are most likely due to variations in several key environmental factors. Specifically, significant differences in temperature (average 15.5^{o}C in 2013, 20.6^{o}C in 2014), depth (average 0.5m in 2013, 0.18m in 2014) , and velocity (average 0.07m/s in 2013, 0.196 m/s in 2014), were found between years. Below, I dissect the main effects of strain and risk treatments on behavioural responses critical to survival.

Changes in activity, or time spent on substrate, strongly indicate antipredator behaviours in Atlantic salmon (Brown *et al.* 1995; Berejikian *et al.* 2003; Leduc *et al.* 2006; Kim *et al.* 2009). Fish initially spent

more time on substrate and were less active at the beginning of the week-long trial. This level of inactivity was consistent with previous examinations of predation threat response by wild juvenile salmon (Leduc *et al.* 2006). For both years, hatchery fish under high predation risk tended to increase time on substrate by the end of the trial period. Similarly Lee & Berejikian (2008), found that under high-risk of predation, fish limited their exploratory behaviour. Overall results suggest that hatchery fish did not improve their use of time on the substrate, which may indicate a failure to thrive in the wild environment.

When faced with increased risk of predation, a common antipredator behaviour of Atlantic salmon is to reduce foraging rate (Gotceitas & Godin 1991; Kim *et al.* 2009). However in this study, no significant changes in foraging rate were seen throughout the trial period, regardless of strain or background risk of predation. However, foraging rate itself (which may include attempts to consume non-food items), may not be a good indicator of foraging success in hatchery-raised fish. For example, Tatara *et al.* (2008) demonstrates that juvenile Brook trout in streams only ingest about 42% of attacked prey items. Therefore, foraging attempts by hatchery fish may have allowed for more learning opportunities, even if there was difficulty identifying or capturing food items in the water column (Rodewald *et al.* 2011).

Juvenile Atlantic salmon living in streams attempt to acquire and maintain territories, optimally balanced in energy acquired for energy expended (Deverill *et al.* 1999). Previous studies suggest the ideal defendable territory size of juvenile Atlantic salmon to be between 0.25 and 1 m^2. Results of the current study find no territories to be larger than 1m^2, with the typical mean territory size being less than 0.2m^2, which is consistent with previous findings (Deverill *et al.* 1999; Steingrímsson & Grant 2008). Small territory size is likely a result of the large number of fish remaining in one feeding station throughout the period of observation, and exhibiting low occurrences of multi-place foraging. Results suggest territories were restricted by the enclosures. Smaller territory sizes were consistent with less foraging stations being used by the focal fish, which agrees with previous studies (Steingrímsson & Grant

2008). Additionally, territorial overlapping seemed more common in hatchery fish, possibly caused by familiarity with crowded environmental conditions. Steingrímsson & Grant (2008) found an increase in foraging stations visited, or station switching, to be associated with lower quality stations, low social rank, or the result of territorial patrolling (Nakano 1995; Johnsson *et al.* 2000). Remaining in one central foraging station may indicate a lack of patrolling, or that high quality foraging stations are inaccessible.

Blanchet *et al.* (2007) found that alarm cue resulted in significant reduction in territory size in Atlantic salmon when combined with a physical cue; however, this study was from a stream channel environment, not *in-situ*. Additionally, Kim *et al.* (2011) found that continual exposure to alarm cues resulted in decreased overall territory size when compared to control habitats for wild YOY Atlantic salmon. My results found that area use was not significantly impacted by the strain or the level of perceived predation risk; however, the average territory size was significantly lower in 2014, compared to 2013. This was likely due to reduced velocity and stream depth between years. In 2014, the velocity of the river was lower and was recorded using surface velocity, compared to 2013, where a flowmeter was used at 50% depth. Deeper, faster flowing water has been shown to encourage fish to travel further to attack prey, or to switch foraging stations (Steingrímsson & Grant 2010). Steingrímsson & Grant (2010) also found that as velocity increased, foraging increased, to a maximum of $0.16 m.s^{-1}$.

Growth rate over the week long period can be used as an indicator of performance, or potential survival during time spent *in-situ* (Deverill *et al.* 1999). Hatchery fish were found to grow significantly less than their wild counterparts. These results agree with the findings of Araki & Schmid (2010), while Malka (2014) found no difference in growth rate between wild and hatchery strains during time spent *in-situ*. Wild-caught fish displayed similar specific growth rate (SGR) regardless of risk level, while hatchery fish under ambient-risk conditions had the smallest SGR. This suggests that increased risk tends to favorably impact the growth of hatchery-raised, but not wild fish. Lack of experience in the natural environment may create an overestimation of risk level, which can result in a disproportionately high

antipredator response when compared to wild-caught fish. This type of response occurs when prey respond with near-maximum intensity to a threat that is perceived above a minimum response threshold (Blanchet *et al.* 2007; Brown, *et al.* 2009; Mitchell *et al.* 2013). As wild fish tailor their antipredator responses due to previous relevant experiences, they are then able to discern the levels of risk presented by a chemical cue without other indicators of predation risk being present (Hazlett 2003; Brown *et al.* 2011b; Ferrari & Chivers 2011). Behavioural response patterns of wild fish are in accordance with accounts of other prey animals that temporally adjust their anti-predator responses depending on risk level; in addition to combining various sensory inputs that convey predation risk in order to more accurately assess danger (Blanchet *et al.* 2007; Ferrari *et al.* 2009a; Chivers *et al.* 2010).

Several studies confirm that while under captive conditions, hatchery fish display higher growth rates compared to their wild counterparts (Jonsson & Jonsson 2006; Fritts *et al.* 2007; Rodewald *et al.* 2011). This is partially due to hatchery fish being fed ad libitum using commercial pellets, which have increased fat content while reducing protein in order to promote rapid growth over the past few decades (Norrgård *et al.* 2014). As a consequence, it is possible that hatchery fish were collected with larger energy reserves, which translated into an increased growth trajectory even after nutritional status was reduced after release into the enclosures (Brown *et al.* 2011a). By the final trial in August 2013, hatchery fish had become much larger (average 1.24g) than their wild counterparts (average 0.99g) compared to the initial trial, when wild fish (average 0.51g) were larger than hatchery (average 0.39g) (M. LeBlanc, personal observation). This increased growth may have caused hatchery fish to be less active after release, often taking up territory in low-flow areas, or hiding under substrate. Reduced activity has been linked to reduced survival, which agrees with previous observations of decreased survival with later release dates (Brown & Day 2002; Salvanes & Braithwaite 2006; Chittenden *et al.* 2010; Homberger *et al.* 2014). Additionally, differences in anti-predator behaviours between hatchery and wild fish under different risk regimes may be an example of compensatory foraging, which produces

fine tuning of behavioural response in populations experiencing predation risk (Kelley & Magurran 2003; Sih *et al.* 2010; Elvidge *et al.* 2014). Ideally, prey animals should adjust their antipredator response to the level of detectable risk, in order to reduce the energetic costs of anti-predator behaviour (Blanchet *et al.* 2007). However, it may actually be beneficial for hatchery fish to overestimate the level of risk and react with more extreme antipredator behaviours. It is less costly, in terms of potential predation, to readjust overestimated threat responses after repeated threat exposure through processes of learned irrelevance and behavioural plasticity, than to risk exposure to predators and potential mortality (Ferrari *et al.* 2009b; Mitchell *et al.* 2013). With these processes, a stimulus will be labelled as neutral when introduced without a negative reinforcement.

In order for conservation and restocking efforts to be successful, the quality of the released fish must be accounted for. Focus should be switched from a quantity based program model ('release more fish'), to one which focuses on the quality of the fish being stocked. Quality should not only encompass the genetic component, by releasing fish from the same genetic stock with limited generations spent in captivity, but should also consider behavioural aspects (Fritts *et al.* 2007; Fraser 2008; Jackson & Brown 2011). A solution would be to allow hatchery fish access to live prey, reduce densities in captivity, and enrich the environment by adding structural complexity, as a form of life-skills training. An alternative would be to release fry into enclosures as early as possible during development, thus creating a type of soft release process which has been shown to be successful with other reintroduced species (Germano *et al.* 2013; Sacerdote-Velat *et al.* 2014). Chemical alarm cues, combined with predator model training, could also normalize the strong anti-predator responses hatchery fish display when presented with potential risk (Brown *et al.* 2001; Wisenden *et al.* 2004; Rodewald *et al.* 2011).

Overall, the *in-situ* experience itself appears to promote similar behavioural responses in both wild caught and hatchery raised YOY Atlantic salmon. Environmental conditions, where the fish acclimate to natural conditions, should be accounted for, and differences between years should be

minimized as much as possible. However, a week-long trial period appears too short to detect major differences in behavioural responses between the two strains. Additionally, a lack of difference may indicate that one generation in the hatchery is not long enough to cause significant differences in behavioural responses. Future work should explore longer times spent *in-situ*, as well as enrichment of the hatchery habitat before placement into net enclosures, thus allowing the hatchery fish many learning opportunities before their final release.

Figures

Figure 1 - Map of Little Southwest Miramichi River, testing occurred just downstream of the indicator in Little Southwest Miramichi in 2013, and just upstream of the indicator in Catamaran Brook in 2014. Modified from (Leduc *et al.* 2006)

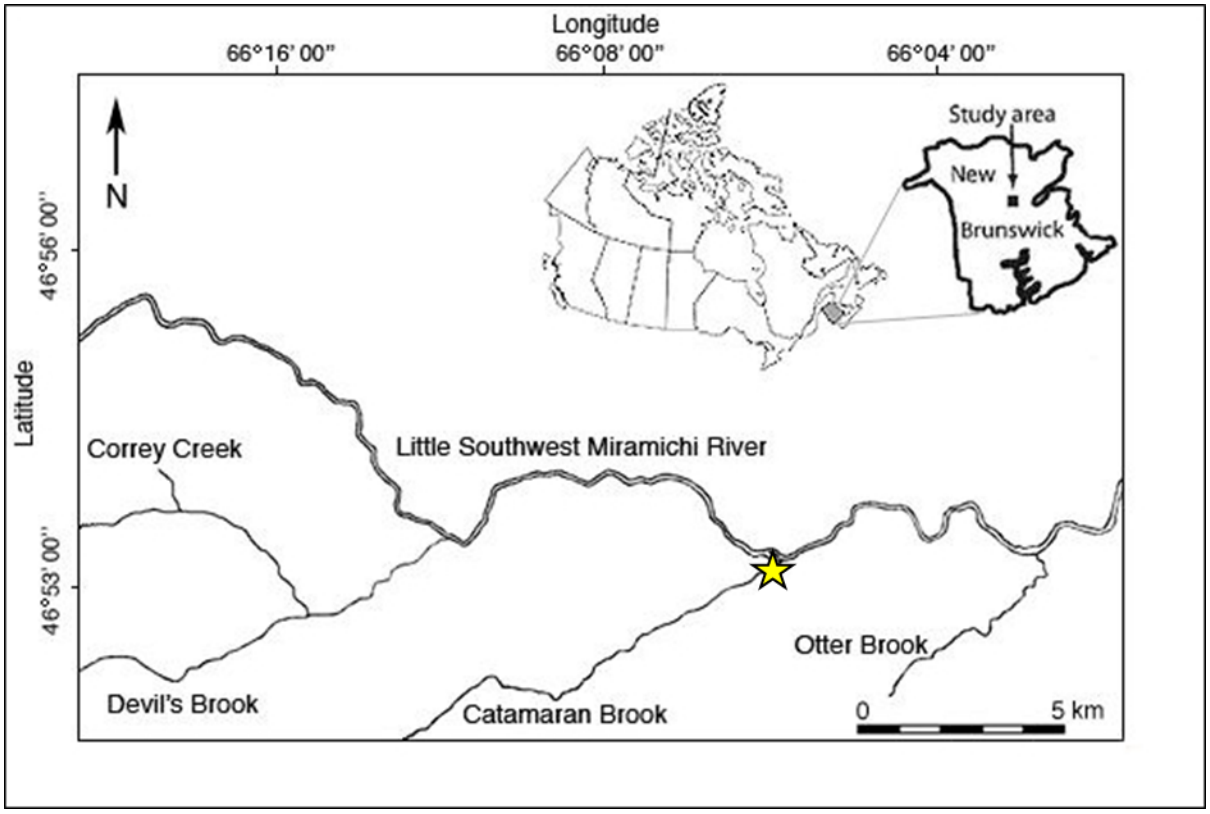


Figure 2 - Mean ± SE. Specific growth rate over trial period divided by wild-caught (WC), and hatchery-raised (HR) strains under alarm cue (AC) or stream water (SW) cue treatment.

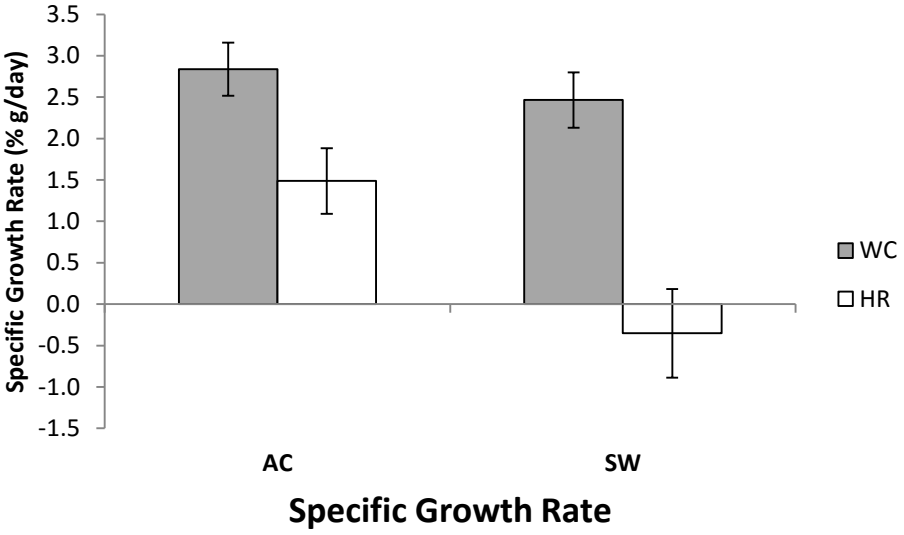
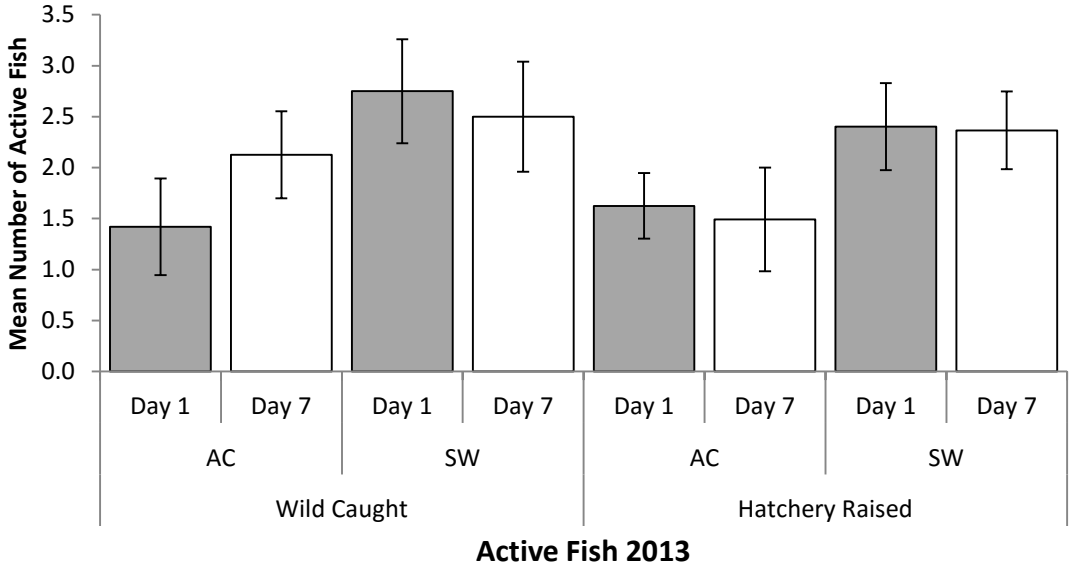


Figure 3 - Mean ± SE For number of active fish over trial period divided by wild-caught (WC) and hatchery-raised (HR) strains under alarm cue (AC) or stream water (SW) cue treatment in A) 2013 and B) 2014.

A)



B)

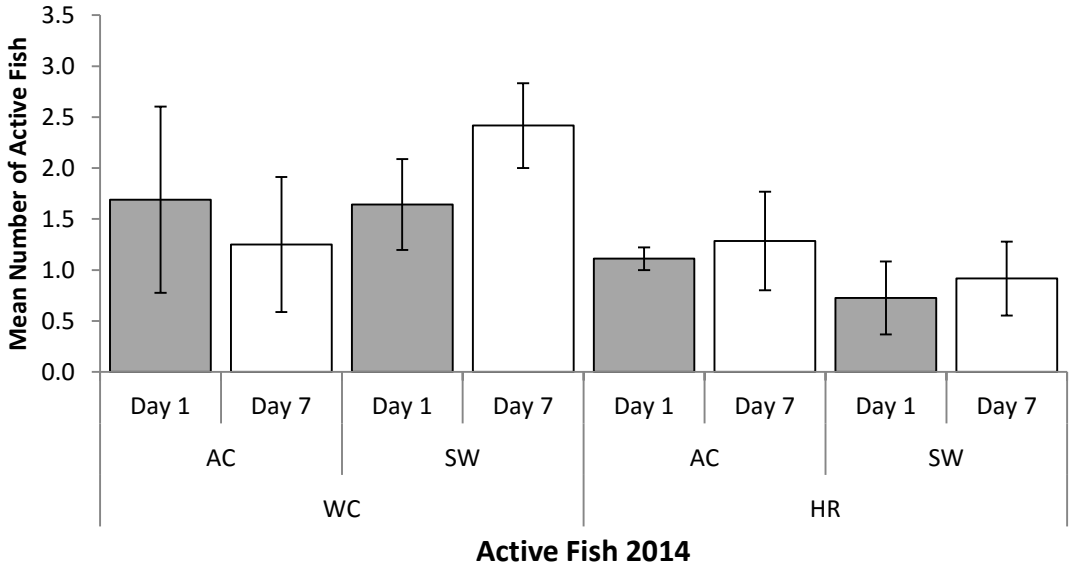
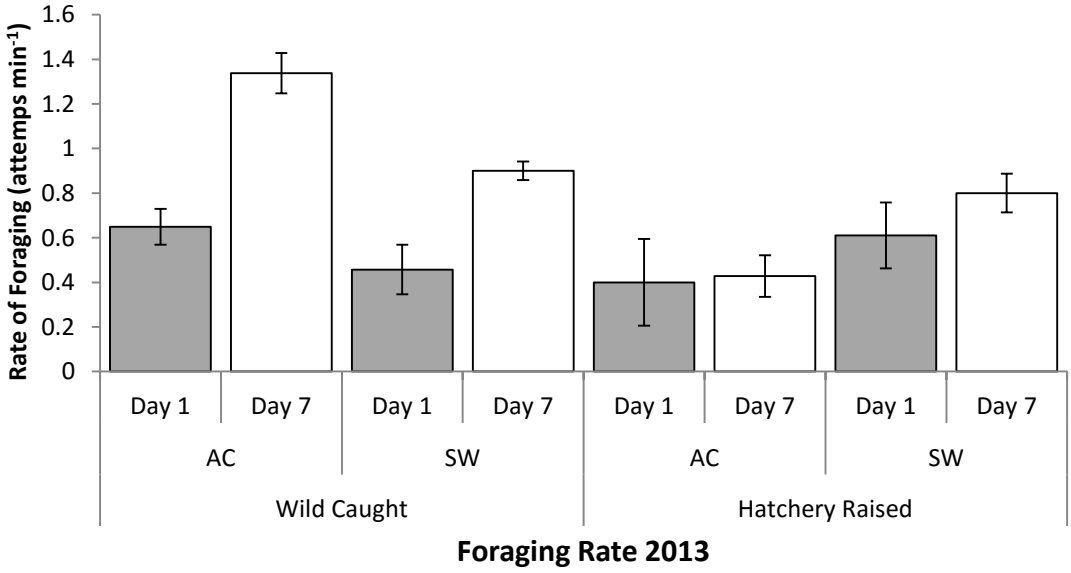


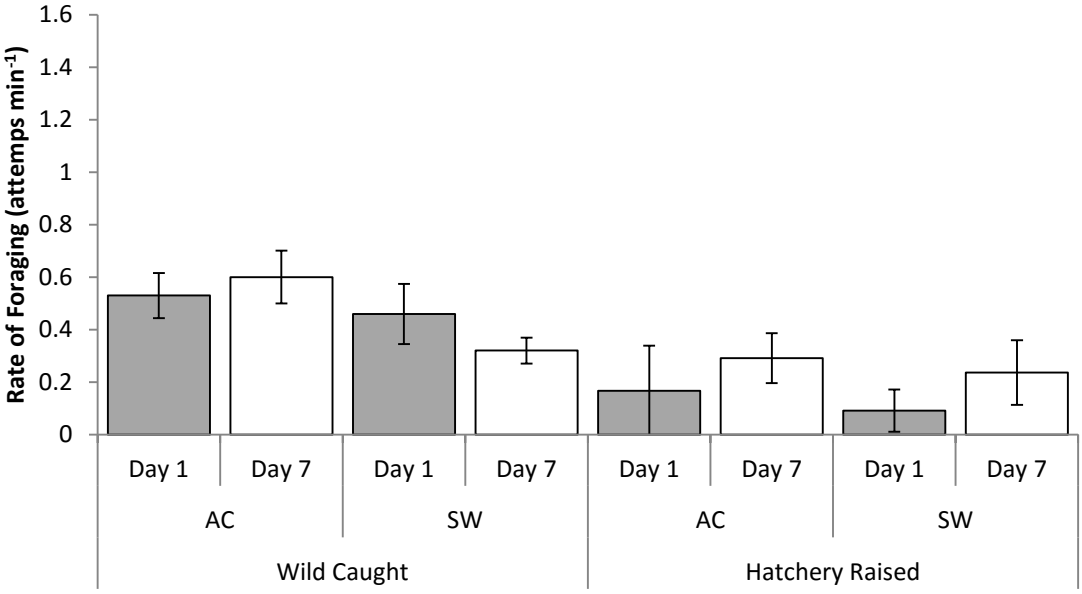
Figure 4 - Bar graph for mean foraging rate (attempts/minute) for wild-caught (WC), and hatchery-raised (HR) strains under high-risk (HR) and low-risk (SW) treatment regimens on day 1 vs. day 7 in A) 2013 and B) 2014.

A)



Foraging Rate 2013

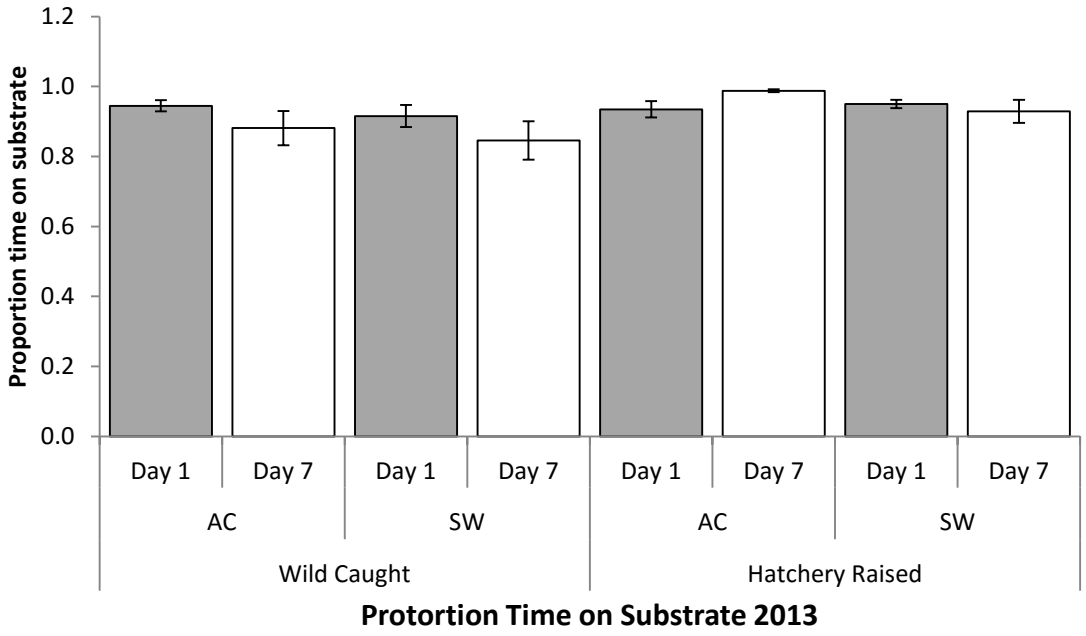
B)



Foraging Rate 2014

Figure 5 - Bar graph for mean ± SE or proportion time on substrate for wild-caught (WC), and hatchery-raised (HR) strains under high-risk (HR) and low-risk (SW) treatment regimens on day 1 vs. day 7 in A) 2013 and B) 2014.

A)



B)

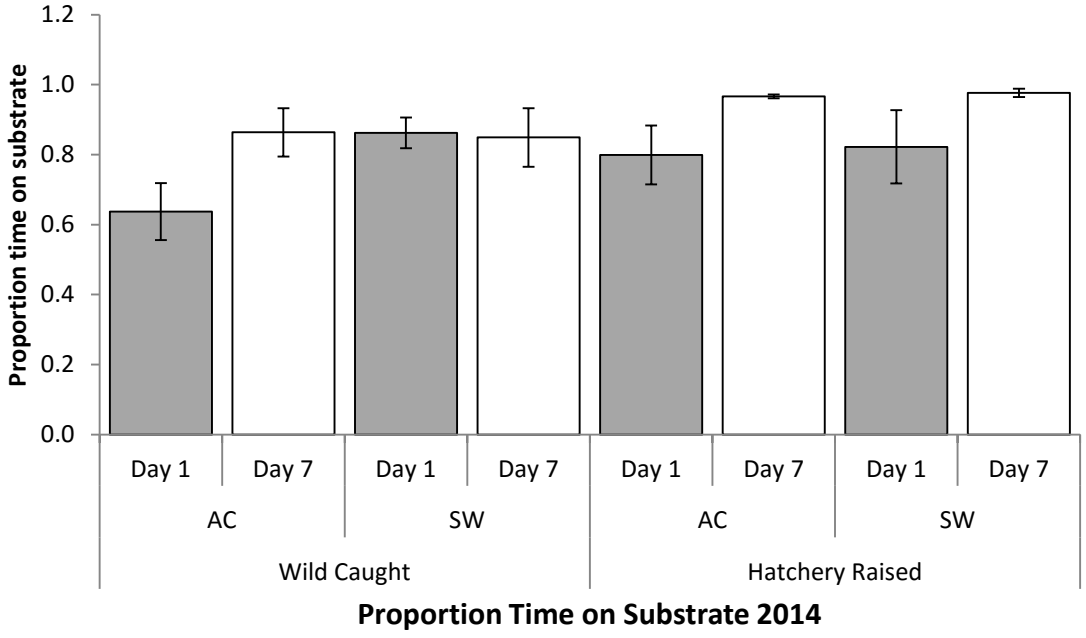
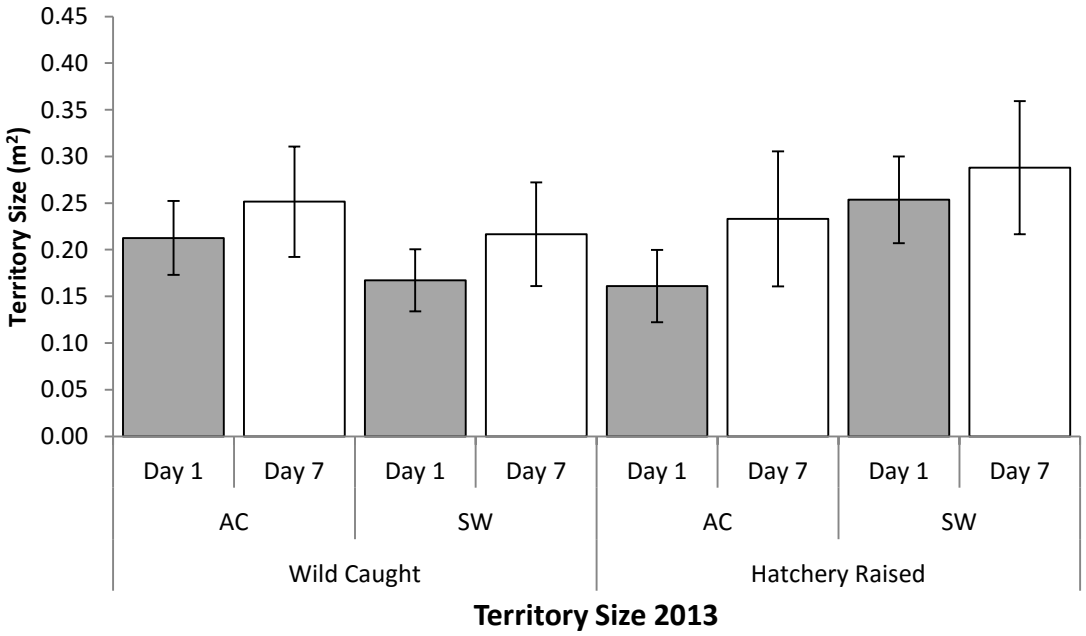
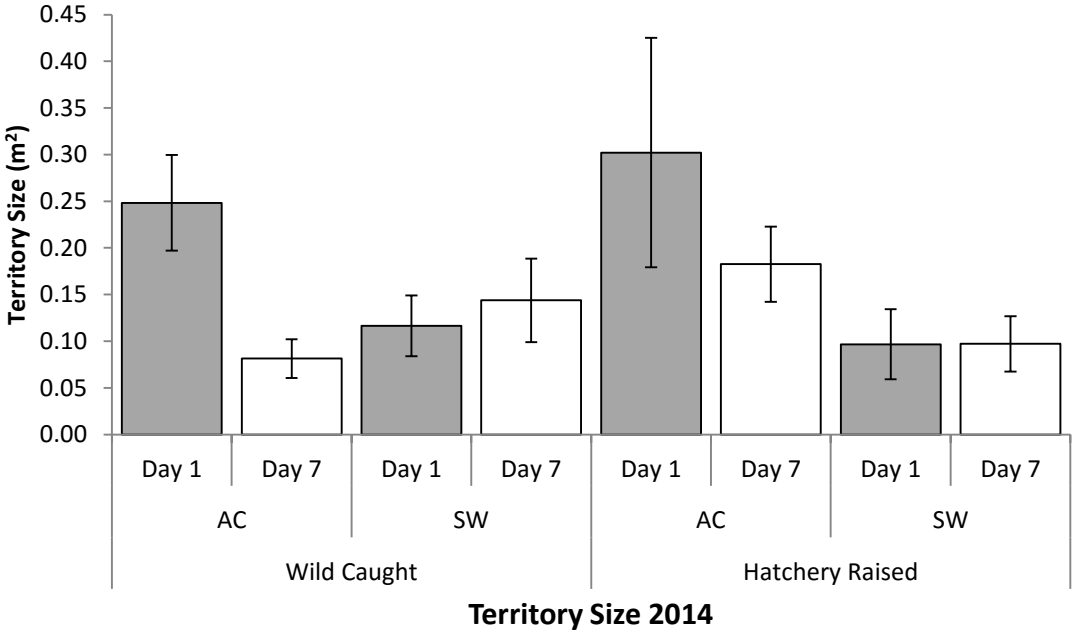


Figure 6 - Bar graph for mean ± SE territory size on days 1 and 7 for wild-caught alarm cue (WCAC), hatchery-raised alarm cue (HRAC), wild-caught stream water (WCSW) and hatchery-raised stream water (HRSW) treatments, for A) 2013 and B) 2014.

A)



B)



Tables

Table 1 - ANOVA results for behavioural response observations on day 1 and day 7. Two-way ANOVAs are used to assess effects on active fish, time on substrate, foraging rate, and territorial area by year, strain, cue and strain*cue interaction.

		Day 1			Day 7		
		F	df	Sig.	F	df	Sig.
Active Fish	Year	4.597	1-28	0.043	3.372	1-28	0.079
	Strain	1.071	1-28	0.311	2.293	1-28	0.144
	Cue	2.302	1-28	0.143	0.006	1-28	0.937
	Strain * Cue	0.516	1-28	0.480	0.794	1-28	0.382
Proportion Time on Substrate	Year	7.137	1-28	0.014	0.277	1-28	0.604
	Strain	0.753	1-28	0.395	1.169	1-28	0.291
	Cue	0.926	1-28	0.346	0.020	1-28	0.888
	Strain * Cue	0.815	1-28	0.376	0.002	1-28	0.969
Foraging Rate	Year	6.751	1-28	0.016	16.46	1-28	0.000
	Strain	0.044	1-28	0.835	4.237	1-28	0.051
	Cue	0.029	1-28	0.866	0.453	1-28	0.507
	Strain * Cue	0.227	1-28	0.638	0.855	1-28	0.365
Area	Year	0.000	1-28	0.989	8.255	1-28	0.009
	Strain	0.313	1-28	0.581	0.231	1-28	0.635
	Cue	0.729	1-28	0.402	0.103	1-28	0.751
	Strain * Cue	0.412	1-28	0.527	0.000	1-28	0.994

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